Using a Null Model to Recognize Significant Co-Occurrence Prior to Identifying Candidate Areas of Endemism

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Using a Null Model to Recognize Significant Co-Occurrence Prior to Identifying Candidate Areas of Endemism

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Recent commentaries on areas of endemism have suggested that these be recognized by the "nonrandom" (e.g., Nelson and Platnick, 1981:56; Morrone, 1994:438) distributional congruence of two or more taxa at some scale of mapping. However, no one has addressed how one might objectively determine the threshold between random and nonrandom co-occurrence for this purpose (Hausdorf, 2002).

Here, we suggest a way to do so that uses a null model to determine the probability that the amount of co-occurrence observed between two taxa could occur by chance relative to the total spatial extent of the data set or a subset of it. We apply the null model to species-in-grid-cell data for the African weevil genus *Sciobius* derived using 2° latitude × 2° longitude cells (Morrone, 1994) and 1° × 1° cells (generated by us from Schoeman's [1983] original range maps). We illustrate the value of the approach in two ways. First, we test the significance of co-occurrence among taxa that are restricted to the areas of endemism that can be recognized using parsimony analysis of endemicity (PAE; Rosen, 1988; Morrone, 1994). Second, we filter out those taxa from the data that are not involved in any instances of significant co-occurrence prior to a reanalysis of the data using PAE to determine its effect on the number of areas of endemism recognized. Additionally, we discuss how graphs that represent instances of significant co-occurrence might be used to recognize biotic elements and consider the scale dependence of the results.

Disputed Use of Co-Occurrence

In recent commentaries, Harold and Mooi (1994) and Hausdorf (2002) suggested that extensive co-occurrence of taxa is neither sufficient nor necessary for the recognition of an area of endemism, although its recognition remains of value to historical biogeography. Harold and Mooi (1994) suggested that areas of endemism can be delineated with overlapping taxon ranges or information independent of taxon ranges (e.g., geological or physiographical features). Evidence independent of taxon ranges must be admissible, they argued, because biotas shaped by vicariance contain ecologically diverse members that might or might not be sympatric at "local" or "regional" scales. Further, areas of endemism should be considered candidate areas of endemism until their historical reality has been tested using the congruence of area cladograms derived from diverse lineages (analogous to the analysis of 1° and 2° homology in biogeography recently reviewed by Morrone, 2001). We accept both of Harold and Mooi's points, because they further tailored the operational definition of areas of endemism to its most common application in historical biogeography. However, the scalar dependence of sympatry is more rigorously discussed by incorporating the scalar dimensions used widely in ecology. These are *extent* and *grain*, the spatial and temporal interval and the subunits of that interval observed, respectively (Wiens, 1989).

In the second commentary, Hausdorf (2002) proposed that extensive co-occurrence does not delimit areas of endemism ("areas delimited by barriers, the appearance of which entails formation of species restricted by these barriers," Hausdorf, 2002:648) but rather it delimits biotic elements ("a group of taxa whose ranges are significantly more similar to each other than to those of taxa of other such groups," Hausdorf, 2002:651). He argued that areas of endemism, thus defined, are not the proper unit in vicariance biogeographic studies, given the confounding effects that range expansions and contractions have on exactly defining their boundaries. Rather, with biotic elements as the units, taxon cladograms should be converted into element cladograms (analogous to area cladograms). Congruence between the element cladograms of different taxa supports their membership in the vicariance element of the biotic elements. We use the term biotic element as defined by Hausdorf (2002), although it is not within the scope of this article to critique their use to construct element cladograms.

The Null Model

The randomization procedure proposed here is a type of null model. Null models are commonly used in ecology (reviewed by Gotelli and Graves, 1996). As a class, these models include pattern-generating models that replace the mechanism(s) thought responsible for some aspect of an observed pattern with a randomization. The randomization produces a null statistical distribution for the aspect of the pattern considered with which the observed values for this test statistic can be compared. Thus, the importance of the excluded explanatory mechanism can be assessed.

In the application of the model described here, phylogeny, ecology, and historical events are excluded as determiners of range locations and shapes, and the range locations and shapes are allowed to vary stochastically within the bounds of a defined area. Range sizes and the spatial extent of the defined area (its size and shape) are held constant. The null model provides an idea of how much co-occurrence is expected by chance when two taxa of the range sizes observed are found within the bounds of the defined area with its unique geometry.

The null model (step 3, below) is implemented in our program package Sigcot version 1.0 (from SIGnificant Co-Occurrence of Taxa). The Sigcot programs are written in Python and can be run on any platform using the Python Interpreter (available at http://www.python.org). Timecritical routines are implemented in ANSI C++ using the GNU C++ compiler (http://www.gnu.org/software/gcc/gcc.html). Sigcot is available from the authors.

Step 1 is to atomize the area to be considered into grid cells of roughly equal size. The extent of this area is defined by the geographic extent of a lineage (*Sciobius*) in our example, but it can be defined in alternative ways. This area is considered to be the present habitable area of the lineage, in the sense that it has been molded by the interplay of physiological, ecological, and historical factors unique to that lineage.

When choosing a grid cell size (the grain of observation), one might try to balance considerations of sampling intensity (to avoid frequent absences due to undercollecting) and internal grid cell heterogeneity (with historical processes in mind in the current application) (Linder and Mann, 1998). Grid cells of hundreds or thousands of square kilometers are common in historical biogeography (e.g., Morrone, 1994; Linder and Mann, 1998; Crisp et al., 2001; Linder, 2001).

Data sets with alternative grain sizes are useful for exploring the dependence of the results on the scale used (e.g., Morrone and Escalante, 2002) and uncovering processes responsible for discontinuities in the pattern observed at alternative scalar dimensions (e.g., contributions to Peterson and Parker, 1998). Variation in the probability assigned by our null model to a pair of co-occurring taxa will almost inevitably change with grain considered, although this is intuitively satisfying. For example, an observation that two species occupy the same 50- $\times$ 50-km grid cell and are restricted to it is judged less significant than the observation that both species co-occur in all 2,500 1-km^2 grid cells in that 2500 km^2 if the grain considered is reduced (and if the habitable area defined for the two taxa is larger than the single 50- $\times$ 50-km grid cell). In this example, although the proportion of the habitable area occupied by the species and the proportion of it in which they overlap has not changed, our surprise that they co-occur to that extent should change.

Step 2 is to score each grid cell for the presence or absence of each taxon of interest. These first two steps are identical to procedures already in use (e.g., PAE and the optimality criterion of Szumik et al., 2002), and thus our method does not require special scoring of the data when used in conjunction with or in addition to these procedures.

Step 3 is to generate a null statistical distribution for the test statistic in each pairwise comparison of range sizes. Stated plainly, the test statistic is the number of grid cells that two ranges overlap (we use range overlap and co-occurrence synonymously here). The null statistical distribution can be generated by (a) randomly choosing two starting cells within the defined area, (b) growing the ranges from these starting cells to the range sizes being compared, (c) making note of the overlap of these two ranges, and (d) repeating steps 3a–3c a large number of times (e.g., 10,000).

Step 4 is to choose a threshold significance level (α) and consult the null statistical distributions to determine instances of significant pairwise co-occurrence in the observed data. Sigcot produces a table of *P* values that includes the results for each pairwise comparison of taxon ranges. The investigator will need to keep in mind the number of comparisons that are relevant to rejection of the particular null hypothesis being tested and adjust the threshold considered significant accordingly.

The generation of random ranges (steps 3a and 3b) is an important part of the procedure, and Sigcot does it in one of several possible ways. Upon choosing a random cell in the grid, the program chooses a second cell adjacent to it (by king's moves; i.e., including those diagonal to it). For choice of the next cell, the program has available to it any cell adjacent to the two chosen cells (also by king's moves). Only those grid cells occupied by at least one taxon in the original data set are available to be chosen. The random choice of a cell and the expansion of the range into contiguous cells within a bounded shape is similar to Jetz and Rahbek's (2001) geometric constraints model, although they allowed the range to expand in only cardinal directions.

Sigcot does not currently deal with disjunctions in the grid cells available for the expansion step (step 3b) in a satisfactory way, and thus we advise the fusion of disjunct cells where it can be done in one or a few justifiable ways. For example, in the *Sciobius* data set, single widespread species occupy satellite cells that are disjunct from the main body of the range, and these cells can be fused with the main body at places where those widespread species occur. In the future, the model could be made to move between disjunctions in the available cells by allowing the expansion step to randomly walk across cells unoccupied by taxa in the data set without considering these to be part of the randomly generated range. This approach, however, can lead to considerably longer computation times.

The expansion step employed here is designed to produce ranges that share aspects of their pattern (e.g., degree of contiguity) with the observed data. It is not meant to mirror the range expansions as they are thought to have occurred (a process). Additionally, if the expansion method is producing ranges that are too dissimilar to those observed, the type I error rate and the power of the test will shift. This will occur, for example, as grain size decreases, ranges will become increasingly disjunct. Although the program does not currently produce disjunct ranges in the expansion step, we are exploring ways that they might be produced based on probabilities calculated from the observed data. At even smaller grain sizes, alternative null models (e.g., an adaptation of Roxburgh and Chesson's [1998] random pattern model) might be more appropriately used. It is not within the scope of this article to validate that this method has acceptable type I and type II error rates with simulated data that meet or incrementally violate its assumptions, although this validation is an important step (Roxburgh and Matsuki, 1999).

Example Involving *Sciobius*

We explored the usefulness of the null model with Morrone's (1994) distributional data set (derived from Schoeman, 1983) for the 47 species of the southern African weevil genus *Sciobius*. We used this data set because it was used previously to introduce two methods for identifying areas of endemism, PAE (Morrone, 1994) and the optimality criterion of Szumik et al. (2002). Morrone scored the presence or absence of each species in 21 2° latitude $\times$ 2° longitude grid cells. We additionally generated a finer scale data set using smaller grain 1° $\times$ 1° grid cells by digitizing Schoeman's (1983) maps and electronically placing the finer scale grid over them (Fig. 1). The 47 species are found in 52 1° $\times$ 1° grid cells (Fig. 2).

In the course of scoring the finer scale data, we discovered errors in the data reported for seven species by Morrone (1994). We made the following corrections to his coarser scale data set (grid cell nomenclature is from Morrone, 1994; see Fig. 1): (1) *S. aciculatifrons* is absent in cell H and present in cell P; (2) *S. cognatus* is absent in cell J; (3) *S. griseus* is present in Namibia, outside of the grid cells labeled by Morrone (designated cells W and X

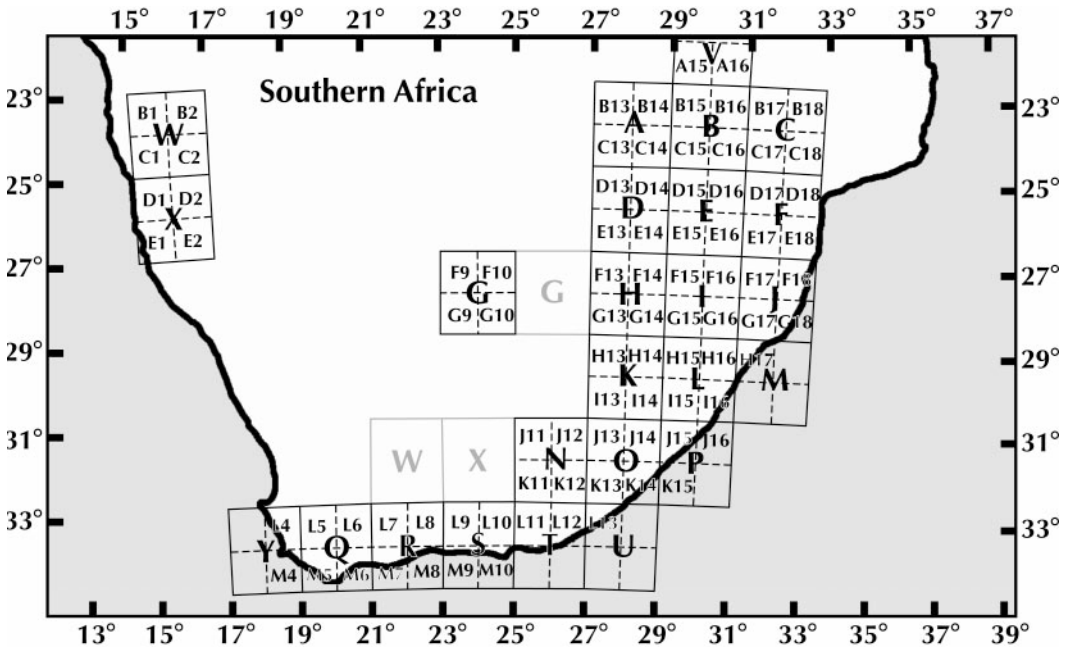

FIGURE 1. Map showing the labeling of grid cells and their equivalency at the two scales of consideration. Single capital letters are used to code the 2° latitude × 2° longitude grid cells, and the nomenclature is the same as that of Morrone (1994) except for the four grid cells not considered by Morrone: cells V, W, X, and Y. An alpha-numeric code is given to the 1° × 1° cells to indicate their position latitudinally (alphabetically) and longitudinally (numerically). Three satellite grid cells (G, W, and X) were fused to the main body of the range for the Sigcot analyses, and the new positions of these are shown with light boxes.

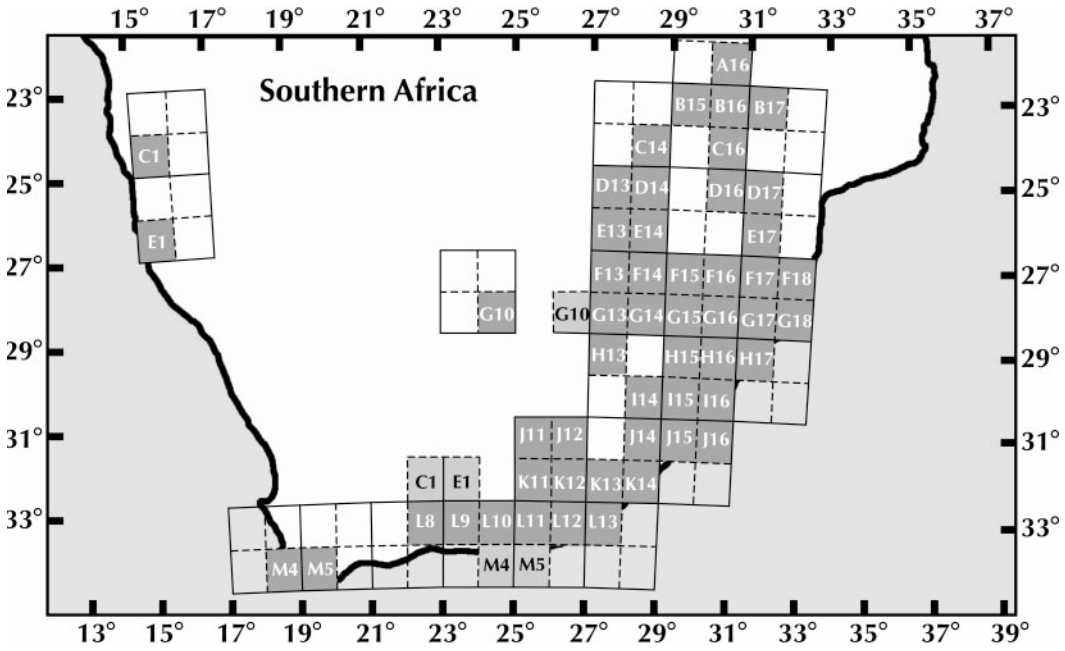

FIGURE 2. Map showing the 1° × 1° grid cells occupied by *Sciobius* (dark shading, white letters and numbers) and the position of five satellite cells fused to the main body of the range for the Sigcot analyses (light shading, black letters, and numbers).

here; Fig. 1); (4) *S. obesus* is present in cells E and F; (5) *S. oneili* is absent in cell R and present in cell U; (6) *S. pullus* is present on the Cape Peninsula outside of the grid cells labeled by Morrone (designated cell Y here; Fig. 1) and is present in cell S; and (7) *S. viridis* is present in the grid cell north of cell B outside of the grid cells labeled by Morrone (labeled cell V here; Fig. 1) and is present in cell D but absent in cells E and H. We closed two disjunctions in the geographic range of *Sciobius* at the coarser scale and four at the finer scale by fusing the satellite grid cells to the main body of the range at locations where the species occupying the disjunct cells (*S. griseus* in cells W and X and their component $1^\circ \times 1^\circ$ cells; *S. horni* in cell G and its component $1^\circ \times 1^\circ$ cells; *S. pullus* in the $1^\circ \times 1^\circ$ cells M4 and M5) are found (Figs. 1, 2).

Sigcot version 1.0 generated null statistical distributions for overlap in each possible pair of range sizes compared at each grain size using 10,000 replicates. At the coarser scale, Sigcot recognized 82 instances of significant co-occurrence involving 29 species at $\alpha = 0.05$ (Fig. 3a). At the finer scale, Sigcot recognized 78 instances involving 28 species (Fig. 3b). Fifty-three instances of co-occurrence were considered significant at both scales, and 25 species were involved in significant co-occurrence at both scales. Probabilities for the observed combinations of range sizes and co-occurrence considered significant at these two grain sizes are provided in Table 1.

TABLE 1. Probabilities assigned to co-occurrence for given range sizes in the *Sciobius* data set as determined by Sigcot version 1.0 for the 2° latitude $\times$ 2° longitude grid cell data and the $1^\circ \times 1^\circ$ grid cell data. All integers refer to numbers of grid cells, and the values are reported in order of ascending P values up to 0.05.

Range size			
Taxon 1	Taxon 2	Co-occurrence	P
$2^\circ \times 2^\circ$ grid cells			
4	4	4	0.0045
3	3	3	0.0114
5	4	4	0.0142
2	2	2	0.0201
4	3	3	0.0225
6	4	4	0.0254
3	2	2	0.0378
1	1	1	0.0383
5	3	3	0.0422
$1^\circ \times 1^\circ$ grid cells			
2	2	2	0.0076
7	5	5	0.0082
7	7	6	0.0091
4	3	3	0.0101
5	3	3	0.0173
7	4	4	0.0186
3	2	2	0.0187
1	1	1	0.0201
4	4	3	0.0238
8	4	4	0.0272
4	2	2	0.0325
2	1	1	0.0375
7	3	3	0.0376
10	7	6	0.0384
7	7	5	0.0403
5	2	2	0.0413
10	4	4	0.0425
7	5	4	0.0433
5	4	3	0.0474

PAE is the maximum parsimony (MP) analysis of grid cells using the presence/absence of taxa as characters with an outgroup that has all of the taxa absent in every cell (Rosen, 1988). In his use of the method to recognize areas of endemism, Morrone (1994:439) suggested that a clade of grid cells can be delimited as an area of endemism when two or more taxa "define" it. We suggest that if the recognition of an area of endemism requires nonrandom distributional congruence (Nelson and Platnick, 1981:56; Morrone, 1994), then in a second step the taxa must be shown to co-occur to an extent that is more than expected by chance at an accepted α. We demonstrate this approach using Sigcot.

In some instances, our criterion of significant co-occurrence can be used to relax a requirement that might be inferred from Morrone's (1994) discussion. That requirement is that the two taxa defining an area of endemism appear as unique and unreversed gains that support the clade of grid cells. There is ambiguity in Morrone's treatment of the cladogram in this respect, because one of the two species (*to*; species abbreviations as described for Fig. 3) used to define his area of endemism 2 is found in some but not all of the grid cells in area 2 (Fig. 4a). However, he did not recognize, for example, grid cells B and E as an area of endemism defined by *pe* (in B and E) and *vt* (only in B; Fig. 4a). We explicitly allow the taxa defining a candidate area of endemism to be gained on different branches of the same clade when they co-occur significantly. Additionally, we seek here to maximize the size of the candidate areas, although one could alternatively seek to minimize them (e.g., recognize cell N as a candidate area in Fig. 4a, rather than recognizing it as part of a large area of endemism 2).

NONA version 2.0 (Goloboff, 1993), as a daughter program of WinClada version 1.00.08 (Nixon, 2002), performed the MP searches for PAE with Morrone's original (uncorrected) data set, the corrected data set, and the finer scale data set (see Appendix, available at http://systematicbiology.org). For these searches, it kept a single tree in each of 100 replicates of tree bisection–reconnection (TBR) branch swappings from random addition trees; the trees kept were then swapped to completion using TBR branch swapping (mult*100;max*). WinClada mapped unambiguous character state changes on a randomly chosen most-parsimonious tree (Figs. 4, 5).

Corrections to Morrone's (1994) coarser scale data resulted in one change in the composition of a clade that he recognized as an area of endemism. His area of endemism 2 would not have included grid cell R and might have included cell U (Fig. 4a and the clade that includes candidate area of endemism 2′ in Fig. 4b; tree statistics are shown in the figures). PAE of the finer scale data resulted in >46,000 most-parsimonious trees (the maximum number saved), and the strict consensus of the trees was poorly resolved (Fig. 5a).

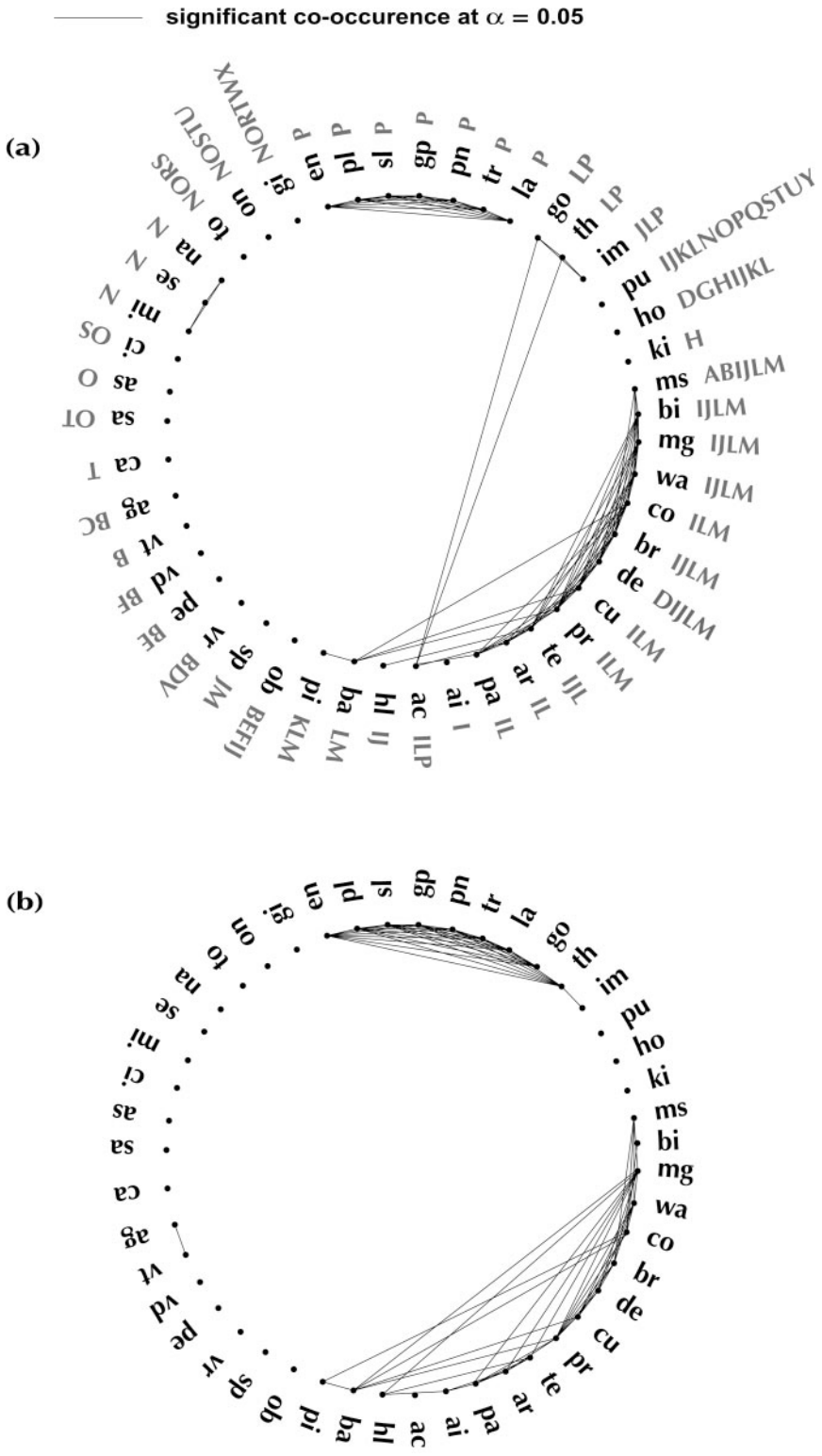

FIGURE 3. Instances of significant pairwise co-occurrence. The pairs of lowercase letters represent the species involved; in most cases, the first two letters of the specific epithet are used. However, in the following cases this scheme was modified because of ambiguity: *ag = angustus; ai = anriae; gp = granipennis; go = granosus; gi = griseus; hl = holmi; mg = marginatus; ms = marshalli; pi = pollinosus; pn = pondo; sa = scapularis; se = schoenlandi; sl = scholtzi; vd = viduus; vr = viridis; vt = vittatus*. (a) Results for the coarser scale data (2° × 2° grid cells). The outer circle of capital letters indicate the grid cells occupied by each species. (b) Results for the finer scale data (1° × 1° grid cells). Grid cells occupied by each species can be found in the Appendix (http://systematicbiology.org).

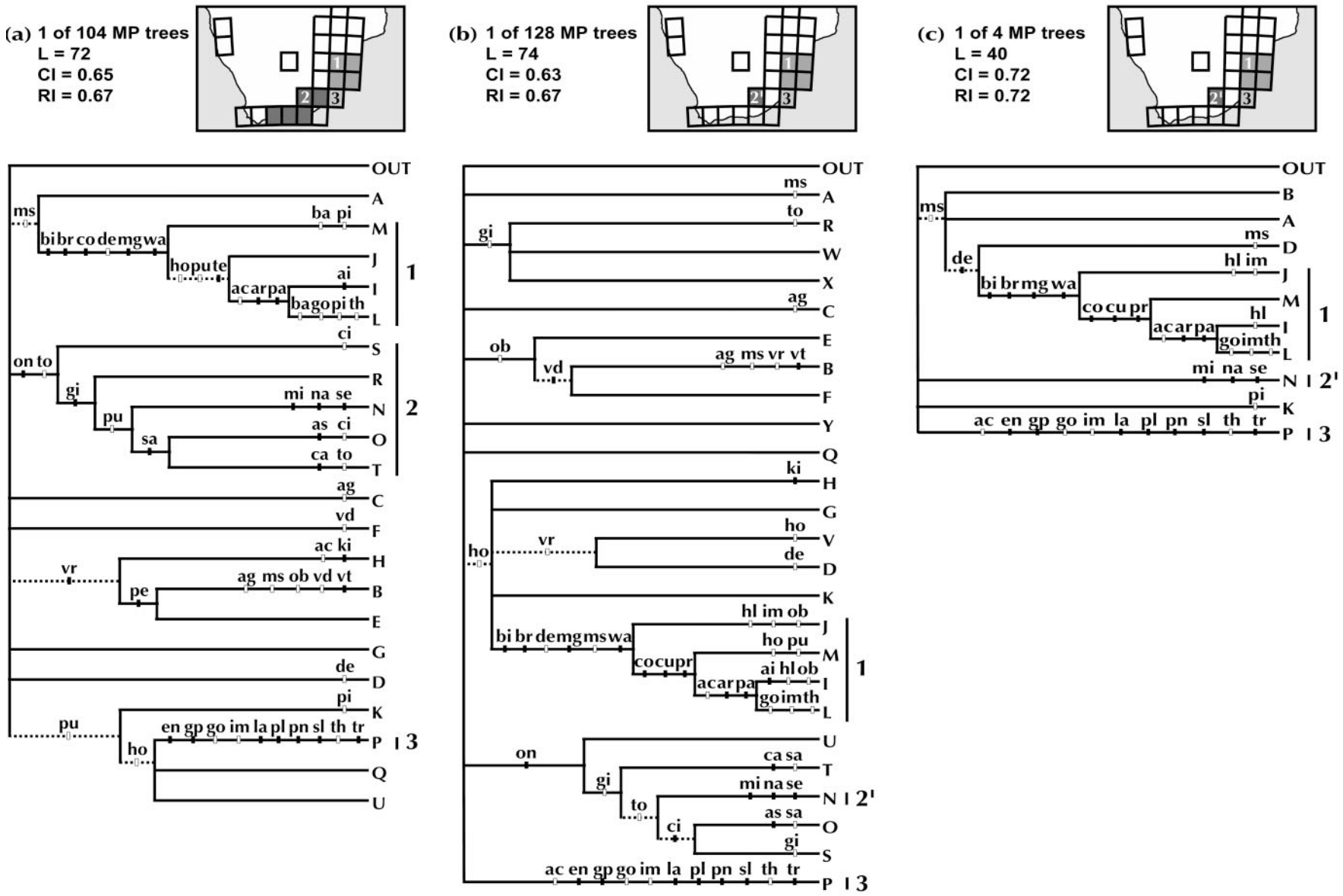

FIGURE 4. Single trees from shortest trees found using PAE on the 2° × 2° grid cell data. Solid bars indicate unique, unreversed gains of a species; open bars indicate parallel gains, a gain that is later lost, or the loss of a species. Only unambiguous gains and losses are shown. Abbreviations of specific epithets are as in Figure 3. Dashed branches collapse in the strict consensus of all shortest trees. Candidate areas of endemism are numbered to the right of the grid cell names, and their geographic positions are shown on the inset maps. L = length; CI = consistency index; RI = retention index. (a) Results from analysis of Morrone's (1994) original, uncorrected data set. (b) Results from analysis of the corrected, unfiltered data set. (c) Results from analysis of the subset of the data that includes only species that co-occur significantly with at least one other species (grid cells left unoccupied removed from the analysis).

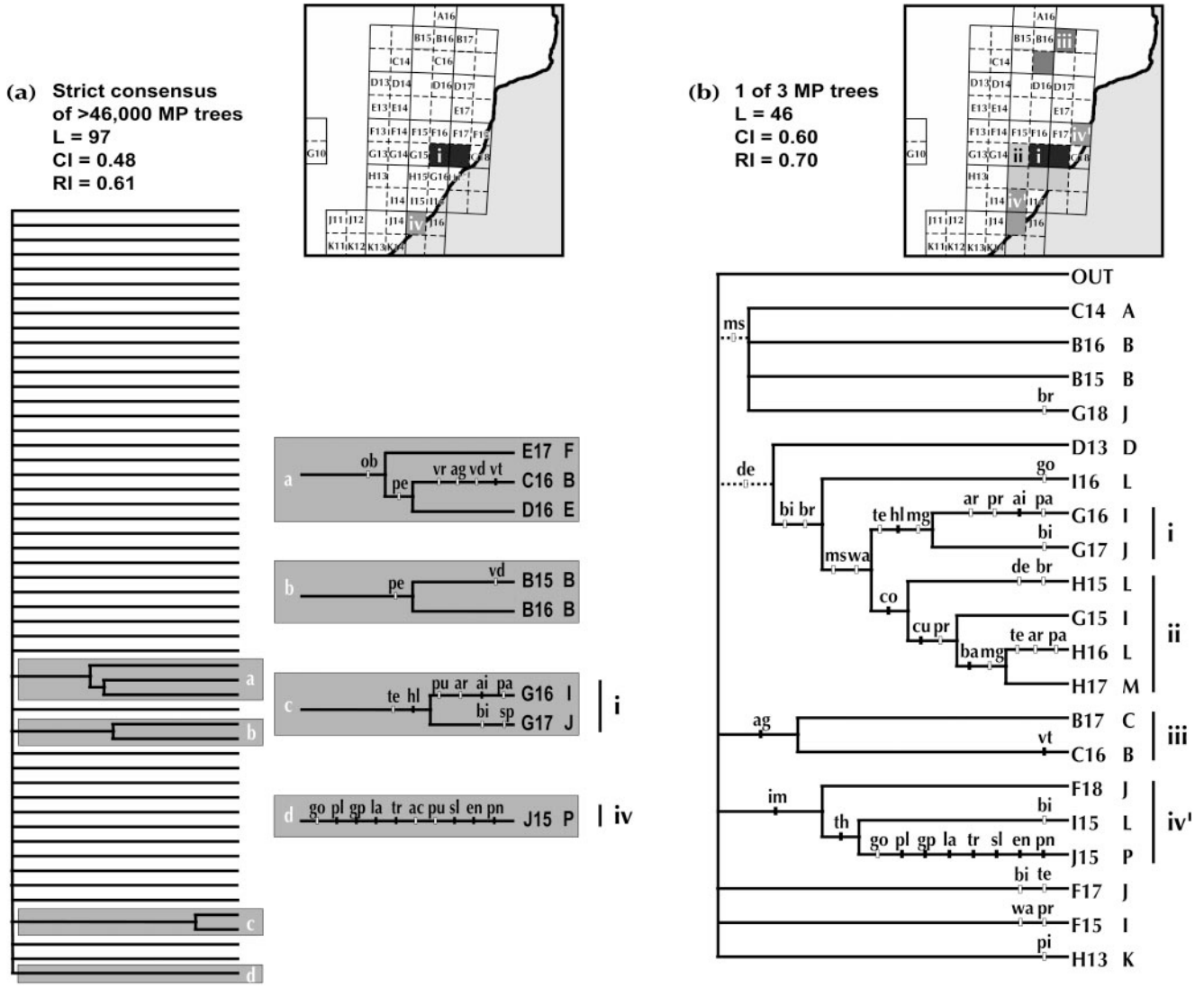

FIGURE 5. Results found using PAE on the $1^\circ \times 1^\circ$ grid cell data. Character state changes, species abbreviations, collapsed branches, candidate areas of endemism, and inset maps used in the same way as in Figure 4. The $2^\circ \times 2^\circ$ grid cell in which the $1^\circ \times 1^\circ$ grid cells are found is given between the $1^\circ \times 1^\circ$ grid cells and the candidate area of endemism labels. (a) Strict consensus of the shortest trees found using the unfiltered data, with character state changes shown from one of the shortest trees in four insets (a–d). (b) Single tree from the shortest trees found using PAE on the subset of the data that includes only species that co-occur significantly with at least one other species (grid cells left unoccupied removed from the analysis).

Three candidate areas of endemism were recovered for the corrected, coarser scale data (Fig. 4b) and two were recovered for the finer-scale data (Fig. 5a). Two of the three areas that Morrone (1994) originally recognized, areas 1 and 3, are supported by significant pairwise co-occurrence among species restricted to them. For example, candidate area 1 is supported by six instances of significant pairwise co-occurrence among the four species (*bi*, *br*, *mg*, and *wa*) that are found throughout and are restricted to the area of endemism (Fig. 4b). The candidate area of endemism is further supported by the significant pairwise co-occurrence of these four species with the three species (*co*, *cu*, and *pr*) found throughout and restricted to three of the four grid cells (M, I, and L) in this candidate area. We reduced Morrone's third candidate area of endemism (his area 2; Fig. 4a) from five cells to one (cell N; candidate area 2′, Fig. 4b) because the probability of co-occurrence among the species (*on*, *ci*, *ca*, *as*, and *sa*) restricted to a larger clade involving these grid cells is not less than $\alpha = 0.05$. In the analysis of the finer scale data, candidate area of endemism i is recognized because of the significant co-occurrence of *hl* and *ai*, and candidate area iv is recognized because of the significant co-occurrence of all 21 pairwise combinations of the seven species restricted to it.

The number of multiple comparisons relevant to rejection of the null hypothesis (that there are not two taxa that significantly co-occur and are restricted to a given clade

of grid cells) will often be much less than $n \times (n-1)/2$, where n is the number of taxa restricted to a clade under consideration. Further, each of the candidate areas of endemism recognized here (Figs. 4, 5) were recognized after a single comparison and thus do not require corrections for multiple comparisons. This is for three reasons. First, the comparisons are done in a directed way (i.e., working from the base of the tree to maximize candidate area sizes or from the terminals to minimize them). When seeking to maximize the size of a candidate area, comparisons begin when the gain of a taxon that is restricted to a single clade of grid cells is found. If there are two gains of this type on the same branch and the taxa gained co-occur significantly, then only this single comparison is necessary. Second, there are certain combinations of results in the multiple comparisons that can be made that are not possible or not likely. For example, if more than two unique and unreversed changes occur on the same branch, all pairwise comparisons of the ranges of these taxa will result in the same conclusion regarding the null hypothesis because the same combination of range sizes and co-occurrence is considered in each case. Additionally, if the null hypothesis is not rejected, it is unlikely to be rejected when these taxa are compared with taxa that are restricted to the clade but gained closer to the tips of the tree. This result makes sense intuitively and is apparent in Table 1, where taxa of range size 4 that overlap by 4 are assigned a P value of 0.0045, those of sizes 4 and 3 that overlap by 3 are assigned a higher P value of 0.0225, and those of sizes 4 and 2 that overlap by 2 are assigned a P value >0.05. Third, once the clade under consideration changes (e.g., by reducing the clade U (T (N (O, S))) to T (N (O, S)); Fig. 4b), the null hypothesis changes, as do the comparisons relevant to that null hypothesis.

Including taxa not involved in significant co-occurrence (as in these first PAE analyses) will not contribute to the recognition of candidate areas of endemism (following the criterion that we propose). More importantly, it could obscure the recognition of candidate areas and lead to the conclusion that these candidate areas are smaller and/or less well supported than might be otherwise recognized. We next explore the effect of filtering taxa that are not involved in significant co-occurrence from the data prior to PAE using the results of the Sigcot analysis.

Removal of species that are not involved in significant co-occurrence at $\alpha = 0.05$ from the coarser and finer scale data sets leaves 15 grid cells unoccupied in the coarser scale data and 32 unoccupied in the finer scale data. These cells were excluded from the respective analyses. For the coarser scale data, PAE recovered 4 shortest trees that each contain the three candidate areas of endemism (two are single grid cells) recognized in the 128 shortest trees from analysis of the unfiltered data (Figs. 4b, 4c). More dramatic are the results for the finer scale data, where PAE recovered 3 shortest trees compared with the >46,000 for the unfiltered data (Fig. 5). Four candidate areas can be recognized in these three shortest trees: area i (also seen in the unfiltered results), the new areas ii and iii, and an area iv′, which is an expanded area iv (from the unfiltered results). Whether the number of candidate areas of endemism recognized in the strict consensus summaries of the MP searches is significantly different from the number expected if the same number of taxa were randomly filtered from the data set is beyond the scope of this commentary. However, the equal or greater number of candidate areas recognized is promising.

Rejection of the null hypothesis that a taxon does not significantly co-occur with any other involves a maximum of one fewer comparisons than the number of taxa in the data set (here $47 - 1 = 46$), and the inflated probability of making a type I error across the multiple comparisons merits consideration. A common approach taken in this situation (e.g., with the Bonferroni method) is to lower the threshold considered significant to guarantee that the probability of making even one type I error is not greater than α. However, this lowered threshold comes at the expense of power, and for this application, making one or a few type I errors (erroneously rejecting the null hypothesis and thus including a species in the PAE analysis) is less serious than making many type II errors (erroneously maintaining the null hypothesis and excluding species from the PAE analysis). Thus, methods that inflate type II error to conservatively control type I error should be used cautiously at this step. For the *Sciobius* data, maintaining the probability of making even one type I error across the multiple comparisons at $\alpha = 0.05$ with the Bonferroni method sets the threshold as low as $\alpha/46 = 0.0011$. None of the values in Table 1 break that threshold, and thus the filtered data sets would be empty. Filtering the data without the Bonferroni correction led to recognition of an equal number of candidate areas of endemism (for the coarse scale data set; Fig. 4) or an increased number of candidate areas (for the finer scale data set; Fig. 5). This result is arguably more satisfying and useful than the absence of a result with the Bonferroni method. Further, it is despite the high probability (very close to 1) that the filtered data sets contained one or more erroneously included species.

The issue of multiple comparisons becomes even more prominent if an investigator wishes to use the graphs of significant co-occurrence (e.g., Fig. 3) to recognize biotic elements. Discrete biotic elements might reasonably be equated with connected, multinode subgraphs when the graph is disconnected (e.g., *mi, se*, and *na* as one biotic element and *en, pl, sl, gp, pn, tr*, and *la* as another; Fig. 3a). Alternatively an investigator might choose to recognize as separate biotic elements subgraphs that meet some threshold of connectivity but are joined by a bridge. Depending upon the null hypothesis, the number of comparisons can grow quite large (to a maximum of 1,081 pairwise comparisons for 47 taxa). We will explore this application of Sigcot elsewhere (Mast et al., in prep.) using the false discovery rate (FDR) approach (Benjamini and Hochberg, 1995). The FDR approach is flexible and has higher power than the Bonferroni method by controlling the proportion of erroneously rejected null hypotheses over the total number of rejected null hypotheses rather than controlling the probability of

making even a single false rejection over all of the tests performed.

Finally, we highlight the value of considering the data at multiple scales (in this case, spatial grain sizes) and the dependence of the results of Sigcot and PAE on the scale chosen (a comparison rarely performed with PAE; Morrone and Escalante, 2002). Sigcot judged about one-third of the instances of significant pairwise co-occurrence at each scale (29 of 82 at the coarser scale; 25 of 78 at the finer) to be significant only at that scale. It also judged 4 of the 29 species involved in significant co-occurrence at the coarser scale to not be involved in it at the finer scale, and 3 of 28 in the reverse comparison. In the PAE analyses, when multiple $1^\circ \times 1^\circ$ cells from the same $2^\circ \times 2^\circ$ cell were grouped into candidate areas of endemism (Fig. 5b), these cells were not always found in the same candidate area. For example, the cells G15 and G16 (both from the $2^\circ \times 2^\circ$ cell I) are found separately in candidate areas i and ii. Similar examples occur in $1^\circ \times 1^\circ$ cells from the $2^\circ \times 2^\circ$ cells J and L. Exploration of alternative scales is unusual in historical biogeography, but these results demonstrate that scale can have a significant effect on the conclusions that might be drawn.

Incorporating Phylogeny, Ecology, and Historical Events

Phylogeny, ecology, and historical events can be incorporated into more sophisticated Sigcot analyses by recognizing classes of taxa in the data set, each with its own inhabitable area. Taxa in a class can be part of the same clade, share similar ecological traits, occupy a broadly defined area of endemism, share some other feature, or have some combination of these attributes. When classes are defined, Sigcot's expansion step takes into account differences in the range of taxa in each class. The range of taxa in a class is taken as an approximation of that class's habitable area, although the result will mean different things depending on the approach taken. Sigcot provides flexibility in defining the habitable area for a class by allowing the inclusion of a dummy taxon in a class with which the area considered habitable can be expanded to a larger size based on additional considerations (e.g., environmental parameters). The value of this differentiation of the data set into classes will be illustrated elsewhere using the banksias of Australia's Southwestern Botanical Province as an example (Mast and Givnish, 2002; Mast et al., in prep.).

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